Vision Research 49 (2009) 262–267

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Asymmetrical perception of motion smear in infantile nystagmus

Harold E. Bedell [a,b,*], Jianliang Tong [a]

[a] College of Optometry, University of Houston, 505 J. Davis Armistead Building, Houston, TX 77204-2020, USA

[b] Center for Neuro-Engineering & Cognitive Science, University of Houston, Houston, TX 77204, USA

ARTICLE INFO

Article history:
Received 29 August 2008
Received in revised form 22 October 2008

Keywords:
Eye movement
Infantile nystagmus
Motion streak
Motion blur
Motion smear

ABSTRACT

Normal observers perceive less motion smear if a target moves in the opposite direction of a smooth eye movement than if the target moves to produce the same retinal image speed in the same direction as the eye movement. This study investigated whether a similar asymmetrical attenuation of perceived motion smear occurs in observers with infantile nystagmus (IN). Observers ($N = 3$) viewed a laser spot that moved for 100 or 125 ms to the right or left at a speed between 5 and 60°/s during the slow phase of jerk IN. After each trial, the observer adjusted the length of a bright line to match the extent of the perceived smear. Across observers, the average duration of perceived smear was 39 and 106 ms, respectively, for relative motion of the laser spot in the opposite vs. the same direction as the IN slow phase. In one observer with periodic alternating nystagmus, the direction of spot motion that produced less perceived smear reversed with an alternation in the direction of the IN slow phase. The reduction of perceived motion smear for relative target motion in the opposite direction of IN slow phases is attributed to extra-retinal signals that accompany IN. As during normal eye movements, the reduction of perceived smear for this direction of relative motion should foster the perception of clarity in the stationary visual world.

1. Introduction

Infantile nystagmus (IN) is characterized by rhythmic back-and-forth eye movements that occur primarily in the horizontal direction. Pendular IN wave forms are composed of alternating smooth eye movements in opposite directions and jerk IN wave forms comprise a smooth eye movement in one direction and a fast saccadic eye movement in the opposite direction. Despite the nearly continuous motion of the retinal image that occurs during IN, individuals with this condition seldom perceive the visual world to be moving (Abadi, Whittle, & Worfolk, 1999; Kommerell, Horn, & Bach, 1986; Leigh, Dell'Osso, Yaniglos, & Thurston, 1988) or smeared (Bedell & Bollenbacher, 1996).

The perception of a stationary visual world in observers with IN is attributed primarily to the action of extra-retinal eye-movement signals, which are thought to neurologically "cancel" the ongoing motion of the retinal image (Abadi et al., 1999; Bedell & Currie, 1993; Goldstein, Gottlob, & Fendick, 1992; Leigh, Dell'Osso, Yaniglos, & Thurston, 1988). In observers with normal eye-movement control, evidence indicates the extra-retinal signals that accompany eye movements also contribute to the reduction of perceived motion smear. Specifically, the extent of perceived smear is less when the motion of the retinal image results from an eye movement than when comparable motion of the retinal image occurs during steady fixation (Bedell, Chung, & Patel, 2004; Bedell & Lott, 1996; Bedell & Patel, 2005; Bedell & Yang, 2001). Because of the inability of observers with IN to fixate steadily, it is not feasible to determine whether extra-retinal signals associated with their nystagmus contribute to the minimal perception of motion smear by making the same comparison. An alternative explanation is that the reduction of perceived motion smear in observers with IN is mediated by adaptive changes that occur in the visual system in response to the nearly continuous motion of the retinal image during visual development (Bedell & Bollenbacher, 1996). Further, when viewing a structured visual field, perceived motion smear also may be reduced in observers with IN by inhibitory spatio-temporal interactions (masking) between nearby visual stimuli, as has been documented in normal observers (e.g., Burr, 1980; Chen, Bedell, & Ögmen, 1995; Hogben & Di Lollo, 1985).

Unlike the attenuation of perceived motion smear that can be attributed to adaptation or masking, the reduction during normal smooth eye movements is asymmetric, occurring only when the eye-relative motion of the stimulus includes a component in the opposite direction of eye movement (Tong, Aydin, & Bedell, 2007; Tong, Patel, & Bedell, 2006; Tong, Stevenson, & Bedell, 2008). Our interpretation of this asymmetry is that the visual system applies extra-retinal eye-movement signals to reduce perceived smear only if the *direction* of ongoing retinal image motion is consistent with that expected from a physically stationary object

* Corresponding author. Address: College of Optometry, University of Houston, 505 J. Davis Armistead Building, Houston, TX 77204-2020, USA. Fax: +1 713 743 2053.

E-mail address: HBedell@Optometry.uh.edu (H.E. Bedell).

0042-6989/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2008.10.019

(Tong, Patel, & Bedell, 2005; Tong et al., 2006). An asymmetrical reduction of perceived motion smear during eye movement therefore represents a potential marker for the involvement of extra-retinal signals. To assess whether the reduction of perceived smear that occurs during normal eye movements and during IN can be attributed to similar neural mechanisms, we asked if perceived smear in observers with IN is reduced preferentially when the direction of retinal image motion is consistent with that of a physically stationary target, i.e., when the eye-relative motion of the target is in the opposite direction of the nystagmus eye movement. In addition, we compared the amount by which perceived motion smear is reduced in observers with IN to results obtained previously during normal eye movements, to determine if the influence of extra-retinal signals is *quantitatively* similar in observers with IN and normal observers.

2. Methods

Three adult observers with jerk IN participated in the experiment, after the procedures were explained to them and each observer voluntarily granted written informed consent. The experimental protocol was reviewed beforehand by the University of Houston Committee for the Protection of Human Subjects. The observers' pertinent clinical and oculomotor characteristics are listed in Table 1. Observer SS has periodic alternating nystagmus (PAN), a form of IN in which the directions of the fast and slow phases reverse every few minutes. Each reversal in the direction of IN is separated by a several seconds when the amplitude of nystagmus is minimal (Abadi & Pascal, 1994; Shallo-Hoffmann, Faldon, & Tusa, 1999). Psychophysical data for observer SS were obtained separately for each direction of the IN slow phase.

The observer sat in a completely dark room in a Tracoustics torsion-swing chair, which was locked in position to prevent any rotation (Bedell & Patel, 2005; Tong et al., 2005). A molded neck brace held the observer's head firmly in position. Visual stimuli were presented at a distance of 64 cm on a translucent cylindrical screen that was attached to the chair. To prevent possible confusion, the stimuli were presented monocularly (right eye for observer MS, left eye for observers SS and DV) and the non-viewing eye was occluded. Before each trial, the observer looked at an illuminated green LED that was attached to the inner surface of the screen, close to the straight ahead direction. When the observer pressed a joystick button to initiate the trial, the LED was extinguished and the observer continued to look straight ahead in the dark. Horizontal eye position was measured using an Applied Science Laboratories model 210 Eye Trac, which was monitored by the laboratory pc computer at a rate of 1000 Hz. Approximately 50 ms after the computer detected a fast phase of nystagmus (based on a velocity criterion of 60°/s), a bright, horizontally moving, 6 min arc spot was projected 2° above the previous location of the fixation LED. The purpose of the delay was to wait for the end of the IN fast phase and the ensuing foveation period, so that the moving spot was presented during the slow phase of IN. The moving spot was produced by a green laser diode, mounted above the observer's head and reflected from a galvanometer-mounted mirror. The luminance of the laser spot was set to approximately 2 log units above it's detection threshold, as measured for a 50-ms flash.

On each trial, the spot moved at a randomly chosen velocity between 5 and 60°/s in the same or in the opposite directions as the slow phase of the observer's nystagmus. The trajectory of the moving spot extended equally to the left and right of the previous position of the fixation LED and its duration was 100 ms (125 ms on some trials for subject MS), to foster presentation wholly during the observers' IN slow phases. Following each presentation of the moving spot, the observer matched the extent of perceived motion smear by adjusting the length of a bright horizontal line that was back projected onto the stationary screen, 2° below the fixation LED. The use of a horizontal matching target is justified by the previous finding that observers with IN perceive minimal motion smear for constantly visible targets (Bedell & Bollenbacher, 1996). To confirm this finding, observer MS and two other observers with horizontal IN matched the perceived length of a constantly visible horizontal bright line, between 0.13° and 1.5° in length, by adjusting the length of a simultaneously visible, vertical bright line. The two lines were separated diagonally on the face of an oscilloscope screen (2.5° center-to-center) and viewed in an otherwise dark room. Table 2 shows that the average matching error for the three observers did not exceed 9.2%, which corresponds to a maximum angular error (for a 1.5° horizontal line) of 8 min arc.

Either 3 or 4 blocks of 40 trials were run for each observer with IN. In addition to monitoring and storing horizontal eye-position signals, the personal computer also controlled presentation of the targets and collected the observers' responses. Examples of the eye and test-spot motion on individual trials are shown for each observer in Fig. 1.

Eye-movement records were inspected off line and trials were rejected if any of the following occurred: (a) presentation of the moving test spot did not occur entirely during an IN slow phase, (b) either the slow-phase eye velocity or the calculated retinal image velocity was less than 5°/s during presentation of the test spot, (c) the slow-phase eye velocity clearly increased while the test spot was presented, or (d) a blink occurred during the presentation of the test spot or within 50 ms of its onset or offset, In addition, trials were rejected for observers MS and SS if the center of the moving test spot's trajectory was more than ±5° from the location of the observer's fovea, as calculated from eye-position calibrations before and after each set of 40 trials. For observer DV, whose eye position in the dark was more variable, the criterion for rejection was relaxed to ±10°. Altogether, 36% of the trials for the three observers were deemed acceptable. For each acceptable trial, the average horizontal eye velocity was determined during the time interval that the test spot was presented. The eye-movement velocity and the physical test-spot velocity on each trial then were combined to calculate the velocity of retinal image motion. We define the relative motion of the test spot to be in the *same* direction as the eye movement when the test-spot velocity with respect to the projection screen is faster than the IN slow-phase eye velocity and in the same direction. Relative motion of the test spot *opposite* the direction of eye movement occurs when the motion of the test spot with respect to the projection screen is in the opposite

Table 1
Characteristics of the observers with IN.

Observer (age)	Refractive correction	Snellen acuity	Wave form	Amplitude[a] (°)	Frequency[a] (Hz)
MS (49)	R: −3.00–2.75 × 019 L: −3.75–2.50 × 010	20/30	Jerk left	7.0	3.0
SS (50)	R: −0.25–1.00 × 165 L: +0.25–1.00 × 165	20/60	PAN[b]	3.5	5.2
DV (47)	R: −0.50–4.00 × 010 L: −1.00–3.50 × 010	20/30	Jerk left	3.1	4.3

[a] Nystagmus amplitude and frequency were determined from eye-position calibration data, obtained by asking the observer to look sequentially at five horizontally separated LED targets.
[b] PAN: Periodic alternating nystagmus.

Table 2
Length of a vertical bright line (in degrees) judged to match the length of a continuously visible horizontal bright line, in three observers with horizontal IN.

Observer	Horizontal line length				
	0.13°	0.25°	0.50°	1.00°	1.50°
MS (±*SD*)	0.13 ± 0.025	0.27 ± 0.039	0.49 ± 0.041	0.93 ± 0.062	1.43 ± 0.131
CR (±*SD*)	0.12 ± 0.015	0.24 ± 0.024	0.49 ± 0.041	1.24 ± 0.067	1.84 ± 0.067
AB (±*SD*)	0.12 ± 0.026	0.25 ± 0.030	0.45 ± 0.055	1.04 ± 0.098	1.64 ± 0.180
Average ± *SE*	0.13 ± 0.003	0.25 ± 0.009	0.48 ± 0.013	1.07 ± 0.089	1.64 ± 0.120

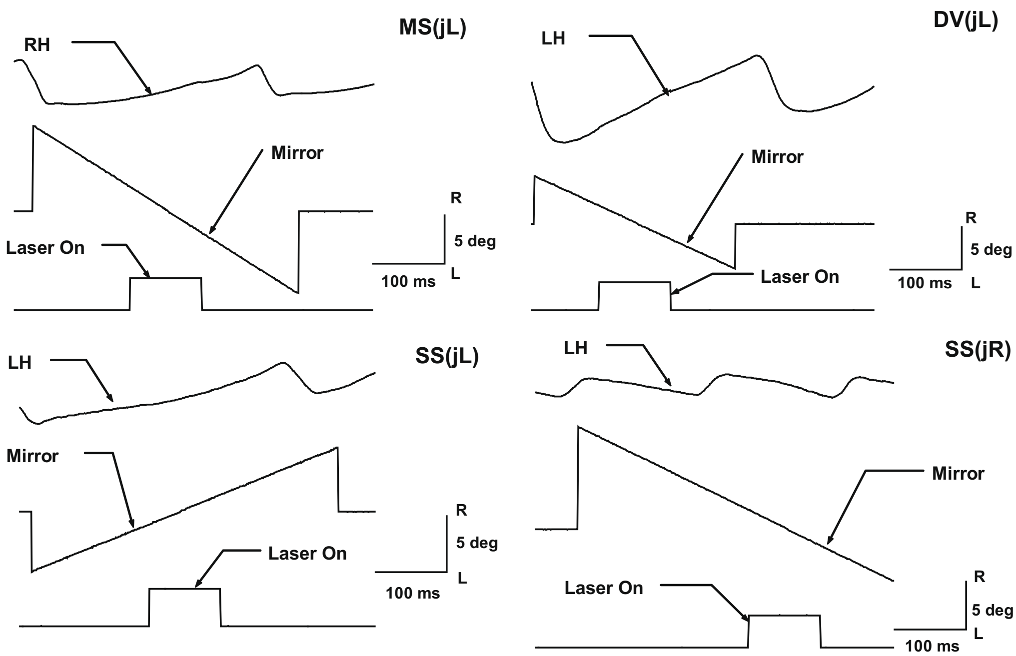

Fig. 1. Examples of test-spot presentations are shown with respect to the IN wave forms of observers MS, SS and DV, recorded on individual trials. Traces are shown for both directions of observer SS's periodic alternating nystagmus. To eliminate any possible effect of mechanical onset transients, motion of the galvanometer-mounted mirror began before presentation of the laser test-spot. Abbreviations: RH: right eye horizontal position; LH: left eye horizontal position; jR, jerk right nystagmus; jL, jerk left nystagmus.

direction as the eye movement or when the motion of the test spot is in the same direction as the eye, but slower.

To allow the data for different eye and test-spot velocities to be compared directly, the extent of matched smear was converted from units of visual angle to units of duration (Bedell & Lott, 1996; Bedell et al., 2004; Chen et al., 1995; Hogben & Di Lollo, 1985), using the equation:

$$\text{Duration of perceived smear} = \text{extent of matched smear } (^\circ)/\text{retinal image velocity } (^\circ/\text{s}).$$

3. Results

The median duration of perceived motion smear is uniformly less when the relative horizontal motion of the bright test spot is in the opposite compared to the same direction as the nystagmus slow phase (Fig. 2). The results shown for observer MS in Fig. 2 are aggregated for stimulus durations of 100 and 125 ms, as the values of perceived motion smear were similar for the two durations (median value ±*SE* for motion *opposite* the IN slow phase = 56.3 ± 7.1 and 51.6 ± 14.0 ms for 100 vs. 125 ms test-spot durations; median values for motion in the *same* direction as the

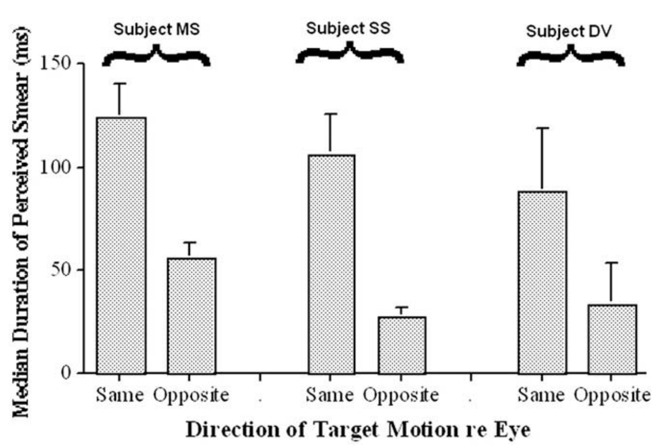

Fig. 2. Median duration of perceived motion smear (±1 *SE*) for three observers with jerk IN, for relative test-spot motion in the same vs. the opposite direction as their IN slow phases. The data plotted for observer MS represent the medians of the combined results for test-spot durations of 100 and 125 ms. The data plotted for observer SS represent the medians for test-spots presented during both leftward and rightward IN slow phases.

IN slow phase = 94.3 ± 28.1 and 128.4 ± 10.7 ms for 100 vs. 125 ms test-spot durations). For the three observers with IN, the difference between the duration of perceived smear for the two directions of test-spot motion is statistically significant (paired $t_{df=2} = 10.10$, $p = .0097$).

A potentially confounding factor is that the range of retinal image speeds was not the same for test-spot motion in the opposite and same direction as the slow phase of the observers' IN. Because we presented the same distribution of test-spot speeds with respect to the projection screen in the same and in the opposite directions as the eye movement, and because the retinal image speed equals the sum of the target and eye velocities, a greater range of *retinal* image speeds was generated when the test spot moved in the opposite direction as the eye. We therefore restricted the comparison of perceived motion smear to an equal range of retinal image speeds (i.e., up to approximately 50°/s) during relative test-spot motion in the same and opposite directions as the IN slow phase. For each observer, the median values of perceived smear are similar to those shown in Fig. 2. Moreover, the difference between the duration of perceived smear for test-spot motion in the same and opposite direction as the IN slow phase remains highly significant (average difference = 63.9 ± 5.2 ms (*SE*); $t_{df=2} = 12.35$, $p = .0065$).

Similarly, the range of eye-movement velocities was greater for the trials with test-spot motion in the opposite vs. the same direction as the slow phase of IN. This occurred because physical target motion in the direction of eye movement produces relative motion in the same direction as the eye when the eye velocity is slow and in the opposite direction as the eye when the eye velocity is fast. However, Fig. 3 shows that the duration of perceived motion smear differs for relative test-spot motion in the two directions, even if the only same range of eye velocities is considered. Previously, we reported that the duration of perceived motion smear for relative target motion in the opposite direction of a normal eye or head movement decreases with the velocity of eye or head movement (Tong et al., 2006, 2008). The data in Fig. 3 suggest that a similar relationship holds in observers with IN for relative test-spot motion in the opposite direction of the nystagmus slow phase ($t_{df=90} = 3.94$, $p = 1.6 \times 10^{-4}$). Note that to quantify this relationship, we discarded outlying estimates of perceived motion smear that substantially exceeded the test-spot duration (i.e., ⩾150 ms).

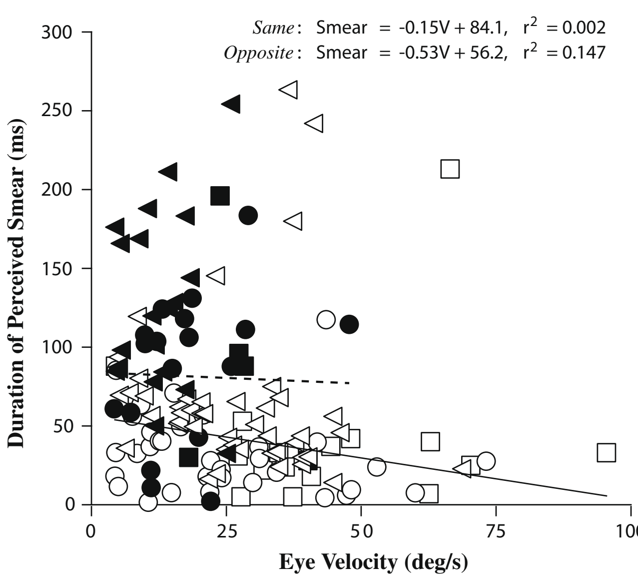

Fig. 3. Median duration of perceived motion smear for observers MS (triangles), SS (circles), and DV (squares) as a function of the eye-movement velocity during relative test-spot motion in the same (filled symbols) and opposite directions (unfilled symbols) of the IN slow phase. To minimize the influence of outliers, the straight lines (dashed for "same" and continuous for "opposite" relative motion) are fit only to durations of perceived motion smear less than 150 ms.

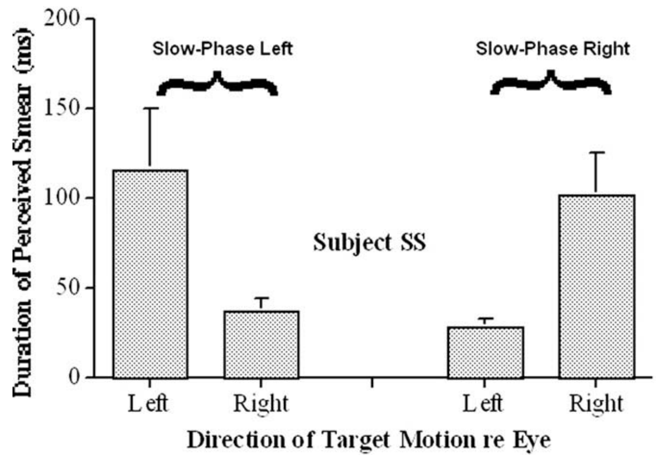

Fig. 4. Median duration of perceived motion smear (±1 *SE*) for observer SS, for leftward and rightward relative test-spot motion during slow phases of jerk right and jerk left IN.

For observer SS, who has PAN, we obtained estimates of perceived smear for motion of the test spot in the same and opposite direction as both leftward and rightward slow IN phases. These estimates are combined in the plot shown in Fig. 2, above, but are presented separately for target spots presented during SS's leftward and rightward IN slow phases in Fig. 4. Clearly, the direction of stimulus motion that produces the smaller duration of perceived motion smear switches according to the direction of the IN slow phase. In particular, relative motion of the test spot in the opposite direction of the ongoing IN slow phase results in less perceived motion smear, compared to when comparable motion of the test spot occurs in the same direction as the IN slow phase.

4. Discussion

In qualitative agreement with previous results obtained during normal smooth eye movements (Tong et al., 2006, 2008), observers with IN report a decreased extent of perceived motion smear when the relative direction of stimulus motion is in the *opposite* direction of the slow phase of IN. For the observers with IN in this study, the duration of perceived motion smear for stimuli that moved in the *same* direction as the IN slow phase was approximately equal to the duration of the moving stimulus. This outcome agrees qualitatively with the results of normal observers, who report no reduction of perceived motion smear compared to fixation, when a stimulus moves in the same direction as a smooth pursuit eye movement. Quantitatively, the reduction of perceived motion smear that we documented in the observers with IN is substantially *more* than the reduction found during eye movements in normal observers, especially for the relatively brief duration of the stimuli used here (Bedell & Lott, 1996; Bedell & Patel, 2005; Bedell et al., 2004; Tong et al., 2006).

The qualitative similarities and quantitative differences between the perception of motion smear during normal eye movements and during the slow phase of IN suggest that the reduction of perceived smear during normal eye movements and IN is mediated by similar, but not identical, neural mechanisms. Because the targets in this study were viewed in an otherwise dark field, visual masking could not contribute to the results. Our observation that the direction of test-spot motion for which perceived motion smear is reduced reverses in an observer with PAN according to the direction of the IN slow phase indicates that adaptation to the previous history of retinal image motion cannot account for the reduction of perceived motion smear. Rather, the perceived extent of motion smear in IN depends on the relative directions of the *ongoing* test-spot and eye motion.

In normal observers, an approximately veridical perception of stable or moving visual targets can be achieved during eye movement by combining the retinal image motion that is produced by the targets with extra-retinal signals (e.g., Freeman & Banks, 1998; Souman, Hooge, & Wertheim, 2006; Turano & Masoff, 2001; von Holst & Mittelstädt, 1950). Previously, we concluded that these extra-retinal signals are responsible also for the observed asymmetrical reduction of perceived motion smear (Tong et al., 2006, 2008). Brenner and van den Berg (1994) documented an analogous asymmetrical contribution of extra-retinal eye-movement signals to the perceived *speed* of the tracked target during smooth pursuit, which depends upon the relative direction of motion of an untracked background stimulus. Specifically, when the untracked background stimulus moves in the opposite direction of the pursuit eye movement, the perceived speed of the pursued target is determined primarily by its retinal image velocity with respect to the background, indicating that the visual system treats the background stimulus as a stationary reference object in space. On the other hand, when the untracked background moves in the same direction as pursuit, the perceived speed of the pursuit target is approximately consistent with the velocity of the eye movement. In this condition, perceived speed is determined presumably on the basis of extra-retinal eye-movement signals because the untracked background is not considered to represent a stationary spatial reference. Several other studies reported an asymmetrical contribution of extra-retinal eye-movement signals to the perceived speed of an untracked *background* stimulus, which also depends on the relative direction of motion between the background and the pursuit target (Freeman, 2001; Turano & Heidenreich, 1999; Turano & Masoff, 2001; Wertheim & van Gelder, 1990). As discussed in detail elsewhere (Tong et al., 2007), these asymmetrical influences of extra-retinal signals on speed perception also can be understood in terms of whether or not the ongoing motion of the retinal image is consistent with a physically stationary background in space.

Extra-retinal eye-movement signals are known also to accompany IN and are credited with promoting perceptual stability (Abadi et al., 1999; Bedell & Currie, 1993; Goldstein et al., 1992; Leigh, Dell'Osso, Yaniglos, & Thurston, 1988). Recently, we proposed that the reduction of perceived motion smear during IN could result from an influence of extra-retinal eye-movement signals on the temporal response speed of the visual system (Bedell et al., 2008a). Both psychophysical (Burr & Morrone, 1996) and physiological data (Reppas, Usrey, & Reid, 2002) are consistent with an increase in the temporal response speed during normal saccades. In addition, Schütz, Braun, Kerzel, and Gegenfurtner (2008) reported a small increase in contrast sensitivity for horizontally oriented chromatic and high-spatial frequency stimuli during pursuit. The results presented here for observers with IN, along with the results presented elsewhere for normal observers (Tong et al., 2006, 2008), imply that the proposed increase in response speed during eye movements should apply specifically to one direction of stimulus motion. Results that are consistent with a unidirectional increase in temporal response speed during normal smooth pursuit were presented recently (Bedell, Tong, Patel, & White, 2008b). However, the substantially greater reduction of perceived motion smear that we found here, as compared to during normal pursuit, suggests that the influence of the extra-retinal signals for IN on temporal response speed is greater.

Because physically stationary objects in the environment undergo relative motion that is in the opposite direction of the eye movements in IN, the present results are consistent with our previous observation that individuals with IN report little or no perceived motion smear for continuously presented visual targets (Bedell & Bollenbacher, 1996; also see Table 2). Although we did not assess the extent of perceived motion smear during the fast phases of our observers' IN wave forms, a previous study indicated that perceived motion smear is attenuated during normal saccades (Bedell & Yang, 2001). On the basis of this result and the phenomenological reports of observers with jerk IN, we assume that the extent of perceived motion smear is reduced during the fast phases of IN as well.

Recently, we showed that the perception of motion smear is reduced also in normal observers during head movements, even when no movement of the eyes occurs with respect to the head (Tong et al., 2006, 2007). Eye movements were minimized in these studies by presenting moving stimuli briefly during suppression of the vestibulo-ocular reflex. In this condition, perceived smear is reduced preferentially for relative stimulus motion in the opposite direction of the observers' head movement. These results indicate that extra-retinal head- as well as eye-movement signals act to reduce the extent of perceived motion smear. This observation is of interest because many observers with IN also make rhythmic head movements, the significance of which is not well understood (Carl, Optican, Chu, & Zee, 1985; Gottlob, Wizov, & Reinecke, 1992; Gresty, Halmagyi, & Leech, 1978). Analogous to our interpretation of the results presented here, we suggest that a possible consequence of the rhythmic head movements in IN may be to further reduce the extent of perceived motion smear.

Acknowledgments

We thank Saumil Patel for technical and conceptual contributions to this study. Portions of this work were presented at the May 2007 meeting of the Association for Research in Vision and Ophthalmology, Sarasota, FL. Support was provided by research Grant, R01 EY05068, and core center Grant, P30 EY07551, from the National Eye Institute.

References

Abadi, R. V., & Pascal, E. (1994). Periodic alternating nystagmus in humans with albinism. *Investigative Ophthalmology & Visual Science, 35*, 4040–4086.

Abadi, R. V., Whittle, J. P., & Worfolk, R. (1999). Oscillopsia and tolerance to retinal image motion in congenital nystagmus. *Investigative Ophthalmology & Visual Science, 40*, 339–345.

Bedell, H. E., & Bollenbacher, M. A. (1996). Perception of motion smear in normal observers and in persons with congenital nystagmus. *Investigative Ophthalmology & Visual Science, 37*, 188–195.

Bedell, H. E., Chung, S. T. L., & Patel, S. S. (2004). Attenuation of perceived motion smear during vergence and pursuit tracking. *Vision Research, 44*, 895–902.

Bedell, H. E., & Currie, D. C. (1993). Extraretinal signals for congenital nystagmus. *Investigative Ophthalmology & Visual Science, 34*, 2325–2332.

Bedell, H. E., & Lott, L. A. (1996). Suppression of motion-produced smear during smooth pursuit eye movements. *Current Biology, 6*, 1032–1034.

Bedell, H. E., & Patel, S. S. (2005). Attenuation of perceived motion smear during the vestibulo-ocular reflex. *Vision Research, 45*, 2191–2200.

Bedell, H. E., Ramamurthy, M., Patel, S. S., Subramaniam, S., Vu-Yu, L. P., & Tong, J. (2008a). The temporal impulse response function in infantile nystagmus. *Vision Research, 48*, 1575–1583.

Bedell, H. E., Tong, J., Patel, S. S., & White, J. M. (2008b). Perceptual influences of extra-retinal signals for normal eye movements and infantile nystagmus. In R. J. Leigh & M. W. Devereaux (Eds.), *Advances in understanding mechanisms and treatment of infantile forms of nystagmus* (pp. 11–22). London: Oxford University Press.

Bedell, H. E., & Yang, J. (2001). The attenuation of perceived image smear during saccades. *Vision Research, 41*, 521–528.

Brenner, E., & van den Berg, A. V. (1994). Judging object velocity during smooth pursuit eye movements. *Experimental Brain Research, 99*, 316–324.

Burr, D. (1980). Motion smear. *Nature, 284*, 164–165.

Burr, D. C., & Morrone, M. C. (1996). Temporal impulse response functions for luminance and colour during saccades. *Vision Research, 36*, 2069–2078.

Carl, J. R., Optican, L. M., Chu, F. C., & Zee, D. S. (1985). Head shaking and vestibulo-ocular reflex in congenital nystagmus. *Investigative Ophthalmology & Visual Science, 26*, 1043–1050.

Chen, S., Bedell, H. E., & Ögmen, H. (1995). A target in real motion appears blurred in the absence of other proximal moving targets. *Vision Research, 35*, 2315–2328.

Freeman, T. C. A. (2001). Transducer models of head-centered motion perception. *Vision Research, 41*, 2741–2755.

Freeman, T. C. A., & Banks, M. S. (1998). Perceived head-centric speed is affected by both extra-retinal and retinal errors. *Vision Research, 38*, 941–945.

Goldstein, H. P., Gottlob, I., & Fendick, M. G. (1992). Visual remapping in infantile nystagmus. *Vision Research, 32*, 1115–1124.

Gottlob, I., Wizov, S. S., & Reinecke, R. D. (1992). Head and eye movements in children with low vision. *Graefe's Archive for Clinical and Experimental Ophthalmology, 234*, 369–377.

Gresty, M., Halmagyi, G. M., & Leech, J. (1978). The relationship between head and eye movement in congenital nystagmus with head shaking: Objective recordings of a single case. *The British Journal of Ophthalmology, 62*, 533–535.

Hogben, J. H., & Di Lollo, V. (1985). Suppression of visible persistence in apparent motion. *Perception & Psychophysics, 381*, 450–460.

Kommerell, G., Horn, R., & Bach, M. (1986). Motion perception in congenital nystagmus. In E. L. Keller, & D. S. Zee (Eds.), *Adaptive processes in visual and oculomotor systems: Proceedings of a conference held in Asilomar, California, June 16–20, 1985* (pp. 485–491). New York: Pergamon Press.

Leigh, R. J., Dell'Osso, L. F., Yaniglos, S. S., & Thurston, S. E. (1988). Oscillopsia, retinal image stabilization and congenital nystagmus. *Investigative Ophthalmology & Visual Science, 29*, 279–282.

Reppas, J. B., Usrey, W. M., & Reid, R. C. (2002). Saccadic eye movements modulate visual responses in the lateral geniculate nucleus. *Neuron, 35*, 961–974.

Schütz, A. C., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2008). Improved visual sensitivity during smooth pursuit eye movements. *Nature Neuroscience, 11*, 1211–1216.

Shallo-Hoffmann, J., Faldon, M., & Tusa, R. J. (1999). The incidence and waveform characteristics of periodic alternating nystagmus in congenital nystagmus. *Investigative Ophthalmology & Visual Science, 40*, 2546–2553.

Souman, J. L., Hooge, I. T. C., & Wertheim, A. H. (2006). Frame of reference transformations in motion perception during smooth pursuit eye movements. *Journal of Computational Neuroscience, 20*, 61–76.

Tong, J., Aydin, M., & Bedell, H. E. (2007). Direction and extent of perceived motion smear during pursuit eye movement. *Vision Research, 47*, 1011–1019.

Tong, J., Stevenson, S. B., & Bedell, H. E. (2008). Signals of eye-muscle proprioception modulate perceived motion smear. *Journal of Vision, 8* (14): 7, 1–6.

Tong, J., Patel, S. S., & Bedell, H. E. (2005). Asymmetry of perceived motion smear during head and eye movements: Evidence for a dichotomous neural categorization of retinal image motion. *Vision Research, 45*, 1519–1524.

Tong, J., Patel, S. S., & Bedell, H. E. (2006). The attenuation of perceived motion smear during combined eye and head movements. *Vision Research, 46*, 4387–4397.

Turano, K. A., & Heidenreich, S. M. (1999). Eye movements affect the perceived speed of visual motion. *Vision Research, 39*, 1177–1187.

Turano, K. A., & Masoff, R. W. (2001). Nonlinear contribution of eye velocity to motion perception. *Vision Research, 41*, 385–395.

von Holst, E., & Mittelstädt, H. (1950). The principle of reafference: Interactions between the central nervous system and the peripheral organs. In P. C. Dodwell (Ed.), *Perceptual processing: Stimulus equivalence and pattern recognition* (pp. 41–71). New York: Appleton Century Crofts.

Wertheim, A. H., & van Gelder, P. (1990). An acceleration illusion caused by underestimation of stimulus velocity during eye movements: Aubert-Fleischl revisited. *Perception, 19*, 471–482.